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Amanita vernicoccora sp. nov. —the vernal fruiting 'coccora' from California

Dimitar Bojantchev[1*], Shaun R. Pennycook[2] & R. Michael Davis[3]

[1]*MushroomHobby.com, 345 Shipwatch Lane, Hercules, CA 94547, USA*
[2]*Manaaki Whenua Landcare Research, Private Bag 92 170, Auckland, New Zealand*
[3]*Department of Plant Pathology, University of California, Davis, CA 95616, USA*
* Correspondence to: *dimitar@pontix.com*

Abstract — We describe *Amanita vernicoccora,* a vernal fruiting species known as the "spring coccora" in California. Sequence analyses of four DNA regions and phenotypic traits demonstrate that *A. vernicoccora,* long considered a pale-colored form of the autumnal fruiting *A. calyptroderma* (the 'fall coccora'), is a unique species. Morphological and genetic data support both species in section *Caesareae.* We also address some nomenclatural and taxonomic intricacies surrounding application of the proper name for the fall-fruiting coccora.

Key Words — *Amanitaceae,* fungal taxonomy, nrLSU, nrITS data

Introduction

The popular name —'coccora' or 'coccoli'— was coined by Italian-Americans in California for two valuable edible mushrooms of genus *Amanita* Pers. collected during the fall and spring. The autumnal fruiting *A. calyptroderma* (referenced here as the 'fall coccora,' Fig. 1a) and the vernal fruiting *A. vernicoccora* (referenced here as the 'spring coccora,' Fig. 1b) are closely related and were for many years considered conspecific seasonal color forms. Both taxa represent subg. *Amanita* sect. *Caesareae* Singer and are close relatives of *A. caesarea* (Scop.) Pers. —the European 'Caesar's amanita'— a popular edible in Europe, especially in Italy. The coccora has a notable thick cottony veil that leaves a distinctive monolithic velar remnant on the pileus. The association with a thick-walled cocoon enveloping the *Amanita* egg is the etymological origin of the popular name.

Due to the perceived conspecificity of the two coccora, the autumnal name was used for both species, currently referenced as either *A. calyptroderma* or *A. lanei*. Both names are still used in various reference materials and field

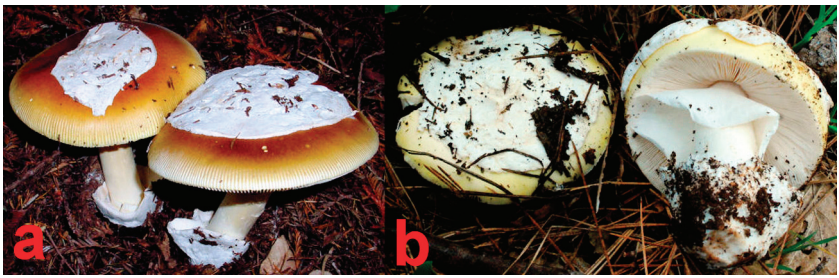

Fig. 1. a) The fall coccora *Amanita calyptroderma*. b) The spring coccora *Amanita vernicoccora*.

guides, and there is general confusion as to which is preferable. The key details of the rich and intricate nomenclatural and taxonomic history surrounding the choice of the proper scientific name for the fall coccora are discussed here.

Nomenclatural and taxonomic history of the fall coccora

Amanita calyptroderma G.F. Atk. & V.G. Ballen, Science, n.s. 29: 944. 1909.

?= *Amanita calyptrata* Peck, Bull. Torrey Bot. Club 27: 14. 1900 [nom. illegit., non Lam. 1783].

≡ *Venenarius calyptratus* Murrill, Mycologia 4: 241. 1912 [nom. nov.].

≡ *Venenarius lanei* Murrill, N. Amer. Fl. 10: 75. 1914 [nom. nov. superfl.].

≡ *Amanita lanei* Sacc. & Trotter, Syll. Fung. 23: 5. 1925 [nom. nov.].

The fall coccora was first validly named as *Amanita calyptrata* (Peck 1900) based on autumnal collections from fir woods in Oregon and notes by Dr. H. Lane. When first published, this name was legitimate, but under the retrospective application of the current International Code of Botanical Nomenclature (ICBN Art. 53.1; McNeill et al. 2006), it is an illegitimate later homonym of *A. calyptrata* Lam. Murrill (1912) "recombined" the name as *Venenarius calyptratus* —under ICBN Art. 58.1, this must be interpreted as a legitimate nom. nov., with priority dating from 1912. Two years later, Murrill (1914) had become aware of the later homonymy of Peck's binomial (illegitimate under the 1907 American Code of Botanical Nomenclature) and published *V. lanei* as a nom. nov. based on Peck's description and typification. However, under ICBN Art. 52.1, the name *V. lanei* was a superfluous (i.e., illegitimate) synonym of *V. calyptratus*, and consequently the "recombination" *Amanita lanei* published by Saccardo & Trotter (Trotter 1925) must also be interpreted as a legitimate nom. nov. under ICBN Art. 58.1.

In 1909 George Atkinson described *A. calyptroderma* (Atkinson 1909a,b) based on autumnal collections, several diagnostic photographs of fresh material, and supplemental notes from Virginia Ballen from Brookdale, Santa Cruz Co., California. According to the Atkinson papers in the CUP Herbarium, the collections were sent from California in fresh condition and

arrived at Cornell University on Dec 7, 1908 with some basidiomata partly decayed. The major elements of the collection notes match the *A. calyptroderma* protologue (Atkinson 1909a,b). The date of the collections, the description, and the photographs published in Atkinson (1909c) leave no doubt that the name *A. calyptroderma* was applied to the familiar fall coccora (Fig.1a, Fig. 10).

Apparently, Atkinson (1909c) was aware of Peck's earlier species and makes a single reference to *A. calyptrata* in the footnote of his description —"closely related to *Amanita calyptrata* Peck, Bull. Torr. Bot. Club 27:14.1909 [sic, = 1900], but differs in color and other characters." Contrary to Atkinson's view, most resident California taxonomists consider *A. calyptroderma* and *A. lanei* (≡ *A. calyptrata*) conspecific. Taxonomically, we believe that *A. calyptroderma* faithfully represents the fall coccora. Moreover, if we accept conspecificity with *A. lanei*/*V. calyptratus* (dating from 1912), *A. calyptroderma* (dating from 1909) has nomenclatural priority. [It should be noted that under the ICBN, until 1981 the correct name for this conspecific taxon was *Amanita calyptrata*, because it remained legitimate and had priority over *A. calyptroderma*. This situation was reversed when the 1981 International Botanical Congress (Sydney) moved the starting point date for agaric nomenclature back from 1821 to 1753, making *A. calyptrata* Peck a nom. illegit.]

Nevertheless, there are lingering doubts about the exact identity of *A. lanei*, as the original description by Peck notes green tinges on the pileus. In our experience, the fall coccora frequently develops olive-brown tints in age or when exposed to colder weather but we would not describe the color as green (Fig. 10c). Olive-brown tints, for example, are commonly observed on specimens from the Sierra Nevada foothills. It is also possible that the stronger color qualification of "green" was used instead of "olive," a common style in many early descriptions. Nonetheless, the green color has been stressed in numerous taxonomic treatments as an important diagnostic character. Zeller (1931) states: "These two species, *A. calyptrata* Peck and *A. calyptroderma* Atkinson and Ballen, are very similar and difficult to distinguish. The main distinction is the greenish tinting of the pileus and gills in *A. calyptrata*..." Hotson (1936) supported this view that the green tints were a key diagnostic character in his treatment of the amanitas of Washington. Although it is unclear whether these authors personally collected green- tinted specimens, we cannot discount the possibility that *A. lanei* refers to a rarely collected unique species from the more northern areas of the Pacific Northwest. This prospect is additionally corroborated by the suggested association of *A. lanei* with fir per its original description. In contrast, the fall coccora is primarily associated with broadleaved trees in California. Therefore, we believe that on both nomenclatural and taxonomic grounds, the correct name for the fall coccora is *A. calyptroderma*.

Murrill (1912, 1914) and Zeller (1931) synonymized *Amanita calyptroderma* and *A. calyptratoides* Peck, although it appears that Murrill never collected or examined either species. Current researchers do not accept this synonymy, and we also consider it to be clearly an error. The macromorphological traits of *A. calyptratoides* —such as the relatively smaller size (4–8 cm), gray-brown to plumbeous pileal colors, and particularly the evanescent to inconspicuous annulus— contrast sharply with the features of *A. calyptroderma* as supported by the very diagnostic original photographs (Atkinson 1909c). The current interpretation of *A. calyptratoides* refers to a small species, common under oaks, with primary distribution of southern California and Mexico (Tulloss 2011).

The conspecificity of fall vs. spring coccora

The conspecificity of the fall and spring fruiting coccora was assumed at the time of the first descriptions and that view generally has not changed. While Peck and Murrill do not seem to have been aware of the existence of a spring fruiting species, Atkinson was and discussed it at length. The original description of *A. calyptroderma* (Atkinson 1909a,b) clearly referenced the fall species based on the time of collection and the colors he specified — "pileus maize yellow to pale chrome yellow." Very soon after that, based on the input of his experienced California correspondent, Virginia Ballen, he offered a more elaborate description of the pileus colors (Atkinson 1909c), including the spring form, "The pileus is a maize-yellow in its bright-colored forms and varies to a pale straw color or Naples yellow (R.) in the vernal forms."

Regarding the vernal fruiting habit of the coccora, Atkinson (1909c) developed an elaborate hypothesis:

> "It occurs in the high Sierras and in the Coast Range. Probably the entire summer season is needed for the growth and extension of the mycelium in the forest mold, so that the huge fruit bodies are developed in late autumn and early spring. While we have as yet no information bearing on the time of origin of the fundament of the fruit bodies, it is likely that all of them are formed during the summer and late autumn, and that the second crop, which appears early in the spring, is composed of plants which have lived through the winter in a partially developed condition. The autumn crop ceases about the last of December, while the spring crop begins about the middle of March."

Contemporary authors of influential field guides in California (Arora 1986, Wood & Stevens 2009) continue to reflect the notion of the conspecificity and seasonal color differences between the fall and spring coccora. At the same time, the awareness that they are likely different species has grown in recent years. Smith et al. (2007) first reported that the fall and spring coccora differ significantly in their ITS sequences.

Materials & methods

Methods for morphological studies and DNA extraction, PCR conditions and primers, and amplicon clean up and sequencing follow Bojantchev & Davis (2011). Collections are stored in the Bojantchev private herbarium or at the University of California herbarium in Berkeley (UC) as noted.

All *Amanita* nrITS and nrLSU sequences from the public databases GenBank (http://www.ncbi.nlm.nih.gov) and UNITE (http://unite.ut.ee/) were downloaded, reviewed, and selected for quality and identification congruity. Sequence alignments were generated with MAFFT v6.821b (Katoh et al. 2002) with the G–INS–i global alignment iterative refinement strategy. No gap opening and extension penalties were set for better resolution of the variable sectors within nrITS, while the default higher penalties were left for the more conserved nrLSU region. The alignments were visually inspected and corrected where needed.

The evolutionary history of 248 *Amanita* nrLSU sequences was inferred using the Maximum Likelihood method based on the Tamura-Nei model as implemented by MEGA5 (Tamura et al. 2007).

Nine *Amanita* sect. *Caesareae* nrITS sequences, representing four taxa, were selected for higher resolution phylogenetic analysis (Fig. 3). *Amanita muscaria* (L.) Lam. was selected as outgroup. Six sequences representing four taxa —the Asian *Amanita hemibapha* (Berk. & Broome) Sacc., *A. caesarea, A. calyptroderma, A. vernicoccora*— were sourced from GenBank. Three sequences of *A. calyptroderma* and *A. vernicoccora* (including the holotype) are from the authors' collections. Two nrITS sequences of *Amanita jacksonii* Pomerl. (GenBank: AY436461, HQ539807) were excluded due to quality and coverage concerns. The evolutionary history was inferred using the Maximum Parsimony method as implemented by MEGA5 (Tamura et al. 2007). The MP trees were generated by the Close-Neighbor-Interchange algorithm with search level 0 in which the initial trees were obtained with the random addition of sequences (10 replicates). The percentage of replicate trees in which the associated taxa clustered together was calculated from a bootstrap test with 1000 replicates. The search resulted in nine most parsimonious trees (length = 187), which differed only in the topology of the terminal nodes.

Phylogenetic results

Four gene regions —nrITS, nrLSU, RPB2, β-tubulin— were sequenced from *A. calyptroderma* (RMD07036, not photographed) and *A. vernicoccora* (RMD07020, Fig. 9b). Direct comparisons of these four gene regions support

Table 1. The four DNA regions sequenced from collections of *Amanita calyptroderma* and *A. vernicoccora*.

DNA regions	*A. calyptroderma* [coll. RMD07036]	*A. vernicoccora* [coll. RMD07020]	BLAST maximum identity index difference
nrITS	GQ250400	GQ250401	4%
nrLSU	GQ250415	GQ250416	2%
RPB2	GQ401358	GQ401359	2%
β-tubulin	GQ401356	GQ401357	4%

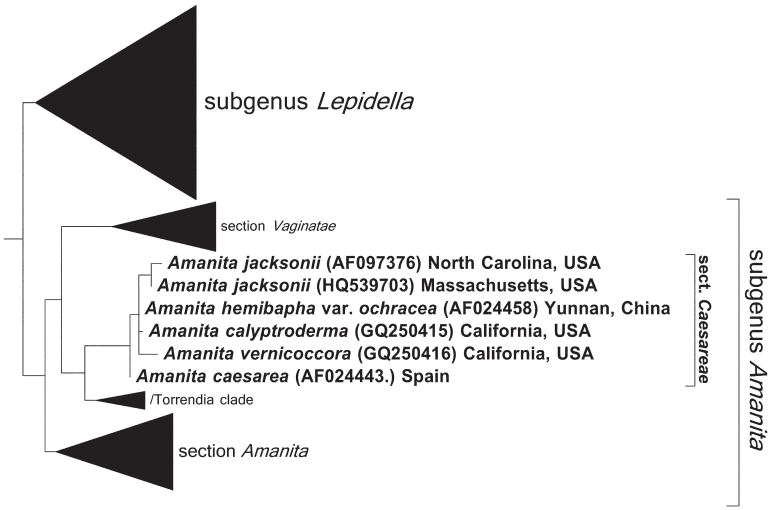

Fig. 2. Phylogenetic tree inferred by maximum likelihood analysis of 248 *Amanita* nrLSU sequences. The tree shows the position of sect. *Caesareae* relative to the collapsed subtrees of the other *Amanita* subgenera and sections. GenBank accession numbers are enclosed in brackets.

the phenotypic and ecological determination that taxonomically they are different species and have been on separate evolutionary paths (Table 1).

The Maximum Likelihood tree (Fig. 2) shows the position of sect. *Caesareae* within genus *Amanita* with the major subgenera and sections compressed. Our research shows strong phylogenetic support for sect. *Caesareae* and generally agrees with Drehmel et al. (1999) and Justo et al. (2010). One most parsimonious MP tree is given in Fig. 3.

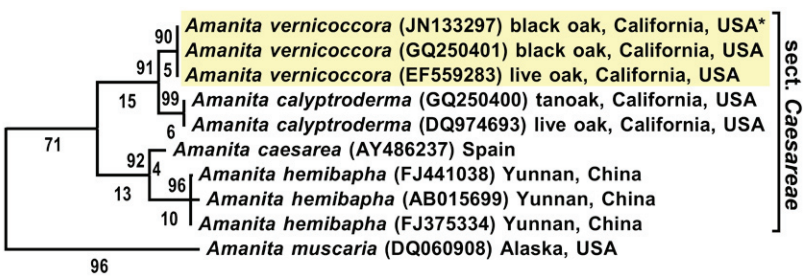

Fig. 3. Phylogenetic tree inferred by maximum parsimony analysis of nine *Amanita* sect. *Caesareae* nrITS sequences with *A. muscaria* as the outgroup. The tree shows the position of *A. vernicoccora* relative to its closest neighbors in sect. *Caesareae*. The percentages of clustered replicate trees based on the bootstrap test (1000 replicates) are shown above the branches while the branch lengths representing estimated nucleotide substitutions are shown below. GenBank accession numbers are enclosed in brackets. The type collection is marked with *.

Fig. 4. *Amanita vernicoccora* DBB00201.

Taxonomy

Amanita vernicoccora Bojantchev & R.M. Davis, **sp. nov.** Figs 4–8

MycoBank MB 561705

Pileo 60–180 mm lato, hemispherico, dein planoconvexo, glutinoso, flavo, margine striato, cum fragmento volvae magno persistento albo. Lamellis confertis, liberis, albis. Stipite 50–140 mm longo, cylindrico, albo. Annulo superiore, striato, albo. Volva ampla, membranosa, crassa. Carne albido. Sapore miti. Species vernalis. Sporis 9–12 × 6–7 µm, late ellipsoideis, hyalinis. Basidiis 42–64 × 11–14 µm, tetrasporigeris, fibulis praesentibus.

Type: USA. California: El Dorado County, Georgetown, Dru Barner Campground, under *Quercus kelloggii,* 21 May 2011, Bojantchev DBB43538 (**Holotype** UC 1860906; Genbank nrITS JN133297).

Etymology: from the Latin *vernus* = vernal and *coccora* = the local name for this mushroom.

Pileus 60–180 mm diam., hemispherical to convex when young, plano-convex to plano-concave with age; margin straight, short striate; color uniform yellow to pale yellow; with a white, monolithic, central velar remnant, cottony thick at first, thinning with age. Lamellae crowded, 10–18 mm broad, white to pale cream, even, seceding to free, lamellulae common. Stipe 50–140 mm long, 15–30 mm wide, cylindrical, white with yellow tints at age, context hollow or stuffed with a cottony or jelly-like substance in buttons. Annulus superior, membranous, pendant, upper surface striate, cottony-thick at first, thinning and collapsing with age, white to pale yellow with age. Volva ample, thick, friable, free, sac-like at first, thinning and collapsing with age, white. Context white to pale yellow. Odor mild at first, pungent with age, frequently interpreted as fishy. Taste mild to pungent. Macrochemical Reactions 5% KOH negative,

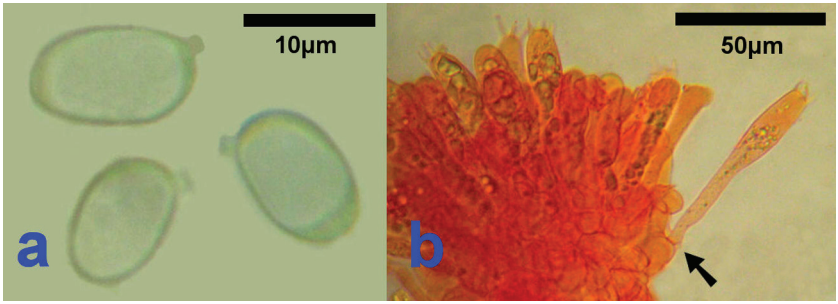

Fig. 5. *Amanita vernicoccora* (UC 1860906, holotype): a) Basidiospores. b) Hymenial layer composed of basidia, basidioles, and subhymenial layer formed of densely packed irregular to pyriform cells; clamped basidia (see arrow). Tissues are stained in Congo Red.

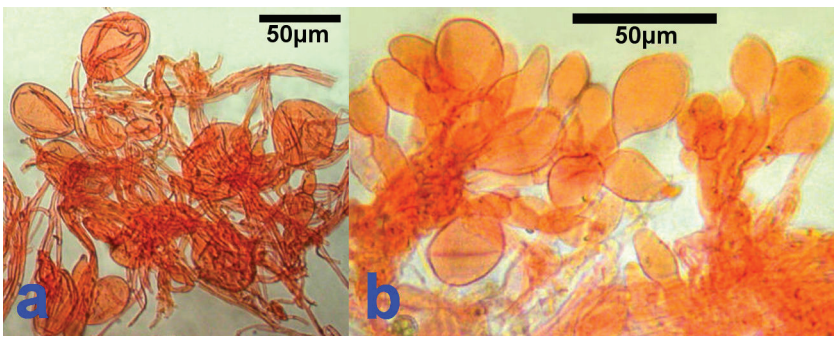

Fig. 6. *Amanita vernicoccora* (UC 1860906, holotype): a) Filamentous and vesiculose cells from the outer surface of the universal veil. b) Inflated cells from the upper surface of the annulus.

10% NH_4OH negative, 3% phenol slowly pinkish-lilac on all surfaces, Guaiac negative, 10% $FeSO_4$ negative. Spore Deposit white.

Basidiospores (8.5–)9.2–11.8(–12.5) × (5.7–)6.2–7.1(–7.5) µm (mean 10.5 × 6.5 µm), Q = 1.43–1.77, Q_{av} = 1.61 (N = 183, 5 basidiomata, 4 collections), broadly ellipsoid, with a prominent lateral apiculus, hyaline, inamyloid. Basidia 42–64 × 11–14 µm, 4-spored, clavate, clamped, sterigmata 4–6 µm long. Subhymenial layer composed of several layers of irregular to pyriform cells 10–30 × 8–22 µm, frequently clamped Lamellar trama divergent, composed of filamentous to swollen hyphae 8–24 µm wide, occasionally clamped. Cystidia not observed. Pileipellis an ixocutis to ixotrichoderm, densely interwoven within a gelatinous matrix, 200–320 µm thick, hyphae 2–7 µm wide, branched, clamped, intracellular pigment. Annulus composed of filamentous cells, 2–6 µm wide with clusters of inflated clavate, pyriform or mucronate cells 25–50 × 16–24 µm, mainly on the upper surface. Universal Veil formed of dense filamentous hyphae 1.5–8 µm wide, clamped, interspersed with vesiculose cells

— on the inner surface: narrow ellipsoid to elongated, 50–120 × 20–50 µm; on the outer surface: broadly ellipsoid to subglobose, 60–180 × 40–150 µm, slightly gelatinized. Stipe Trama acrophysalidic, composed of filamentous hyphae 2–8 µm wide and inflated hyphae 50–150 × 20–46 µm, occasionally clamped.

Habitat and distribution — *Amanita vernicoccora* fruits in the late winter and spring and is apparently restricted to California. Along the coast and in the lower elevations of Sierra Nevada (<2000 feet) it fruits in February–March and is known to associate with evergreen oaks such as live oak (*Quercus agrifolia* Née), interior live oak (*Quercus wislizenii* A. DC.) and blue oak (*Quercus douglasii* Hook. & Arn.). Likely associations are also to Pacific madrone (*Arbutus menziesii* Pursh) and manzanita (*Arctostaphylos manzanita* Parry). Infrequently, *A. vernicoccora* fruits in the northern coastal areas where it is likely associated with tanoak (*Notholithocarpus densiflorus* (Hook. & Arn.) Manos et al. This species is far more common in the foothills of the Sierra Nevada and Shasta Cascade range in May–June where the primary association in the lower elevations (2000–4000 feet) is with the deciduous black oak (*Quercus kelloggii* Newb.). At higher elevations *A. vernicoccora* may switch association to conifers, but we have not seen it outside of the range of the black oak (≤6000 feet).

Additional collections examined: **USA. California**: Amador County, Indian Grinding Rock State Park, elev. 2400 ft, under black oak, 17 May 2009, Davis RMD07020 (Genbank: nrITS GQ250401, nrLSU GQ250416, RPB1 GQ401359, β-tubulin gene GQ401357); El Dorado County, Georgetown, Dru Barner campground, elev. 2540 ft, under black oak, 26 May 2011, Davis RMD110003; 29 May 2011, Bojantchev DBB43625; Eldorado National Forest, Crystal basin area, near Union Valley Reservoir, elev. 4870 ft., under mixed conifers and black oak, 2 Jun 2006, Bojantchev DBB00118; Calaveras County, Stanislaus National Forest, off Hwy. 120 and Hardin Flat Road exit, elev. 3600 ft., under mixed conifers and black oak, 27 May 2006, Bojantchev DBB00102; Stanislaus National Forest, off Evergreen Rd, elev. 4100 ft. under mixed conifers and black oak, 22 May 2006, Bojantchev DBB00099; Siskiyou County, Dunsmuir, off Hwy 5, near Dunsmuir airport, elev. 2300 ft. under black oak, 31 May 2008, Bojantchev DBB00201; Marin County, Marin Watershed, off Bolinas-Fairfax Rd., elev. 800 ft. under live oak, 13 Mar 2008, Bojantchev DBB07809.

Fig. 7. *Amanita vernicoccora:*
a) UC 1860906, holotype. b) DBB07809 under live oak in the California coastal range.

Fig. 8. *Amanita vernicoccora* — a study in the development of the basidiocarp: a) Expanding button, note the jelly like substance in the stipe context, which later turns cottony or leaves it hollow. b) Note the thick cottony universal veil and the striate upper surface of the annulus. c) Note the thinning of the universal veil on pileus, friable volva and collapsing annulus.

Fig. 9. *Amanita vernicoccora* collections: a) RMD110003. b) RMD07020.

Fig. 10. *Amanita calyptroderma*, the fall coccora: a) DBB00347. b) DBB00393. c) DBB00491 shows the frequent olive tinges on the pileus due to exposure to cold weather.

Discussion

Both *A. vernicoccora* and *A. calyptroderma* are beautiful species, distinguished by a thick, cottony, white velar remnant on the pileus that remains whole into maturity. This feature makes them among the easier amanitas to identify. The edibility of the fall coccora, *A. calyptroderma*, was extolled by both Peck (1900) and Atkinson (1909a), who made references to its gastronomical virtue.

While considered conspecific, *A. vernicoccora* also was presumed edible and is widely collected for the table. Even though practical experience has shown that both coccora are relatively safe choices as edibles, confusion with other toxic *Amanita* species do occur and the possibility of dangerous misidentification must be stressed. The standard word of caution is that several reliable taxonomic factors must be evaluated before an *Amanita* collection is deemed safe for consumption.

The greatest danger posed by the pale spring coccora is misidentification with members of the deadly toxic sect. *Phalloideae* (Fr.) Quél. —*Amanita ocreata* Peck and *A. phalloides* (Fr.) Link, which also associate with oaks throughout California. *Amanita ocreata* is a native species, while *A. phalloides* is an import from Europe that has found favorable conditions and spread widely in California (Pringle et al. 2009). Both can have a large patch of universal veil on the cap (Fig. 11). In southern California, *A. ocreata* develops a much more

Fig. 11. Dangerous look-alikes of *A. vernicoccora:* a) The deadly toxic *Amanita ocreata* fruits in the spring under oaks. b) The deadly toxic *Amanita phalloides* is a native of Eurasia, but a recent import to California that fruits abundantly under oak in late fall and winter.

Fig. 12. Dangerous look-alikes of *A. vernicoccora:* a) The toxic *Amanita gemmata* gr. b) The toxic *Amanita aprica* is frequently found with *A. vernicoccora* in the Sierra Nevada foothills. The minutely broken velar remnants on the pileus contrast with the monolithic veil remnant of the spring coccora.

yellowish pileal coloration, which may further confound field identification. Attention needs to be paid to all features of the basidiocarp, particularly to the almost complete absence of striations on the pileal margin of the *Phalloideae* species.

Other yellow species that can be mistaken for *A. vernicoccora* are in the *Amanita gemmata* (Fr.) Bertill. clade, or gemmatoid amanitas (Fig. 12a), which fruit in both the fall and spring in California. They also are toxic. In the Sierra foothills, *A. vernicoccora* frequently co-occurs with *Amanita aprica* J.E. Lindgr. & Tulloss (Fig. 12b). One key feature separating the two species is the manner in which the veil of gemmatoid amanitas breaks into many small patches and warts.

An extensive iconography of *A. vernicoccora* is available at http://www.mushroomhobby.com.

Acknowledgements

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Literature cited

Arora D. 1986. Mushrooms demystified: A comprehensive guide to the fleshy fungi. Ten Speed Press. Berkeley.

Atkinson GF. 1909a. A new edible species of *Amanita*. Science n.s. 29: 944. http://dx.doi.org/10.1126/science.29.754.944

Atkinson GF. 1909b. Preliminary notes on some new species of *Agaricaceae* and *Clavaria*. Ann. Mycol. 7: 365–376.

Atkinson GF. 1909c. A remarkable *Amanita*. Bot. Gaz. 48: 283–293. http://dx.doi.org/10.1086/330013

Bojantchev D, Davis RM. 2011. *Cortinarius xanthodryophilus* sp. nov. — a common *Phlegmacium* under oaks in California. Mycotaxon 116: 317–328. http://dx.doi.org/10.5248/116.317

Drehmel D, Moncalvo J-M, Vilgalys R. 1999. Molecular phylogeny of *Amanita* based on large-subunit ribosomal DNA sequences: implications for taxonomy and character evolution. Mycologia 91: 610–618. http://dx.doi.org/10.2307/3761246

Hotson JW. 1936. The *Amanitae* of Washington. Mycologia 28: 63–76. http://dx.doi.org/10.2307/3754068

Justo A, Morgenstern I, Hallen-Adams HE, Hibbett DS. 2010. Convergent evolution of sequestrate forms in *Amanita* under Mediterranean climate conditions. Mycologia 102: 675–688. http://dx.doi.org/10.3852/09-191

Katoh K, Misawa K, Kuma KI, Miyata T. 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. Nucleic Acids Res. 30: 3059–3066.

McNeill J, Barrie FR, Burdet HM, Demoulin V, Hawksworth DL, Marhold K, Nicolson DH, Prado J, Silva PC, Skog JE, Wiersema J, Turland NJ. 2006. International Code of Botanical Nomenclature (Vienna Code). Adopted by the Seventeenth International Botanical Congress, Vienna, Austria, July 2005. Regnum Vegetabile 146. 568 p.

Murrill WA. 1912. The *Agaricaceae* of the Pacific Coast II. Mycologia 4: 231–262.

Murrill WA. 1914. (*Agaricales*) *Agaricaceae* [pars]. North American Flora 10: 1–76.

Peck CH. 1900. New species of fungi. Bull. Torrey Bot. Club 27(6): 14–21. http://dx.doi.org/10.2307/2477738

Pringle A, Adams RI, Cross HB, Bruns TD. 2009. The ectomycorrhizal fungus *Amanita phalloides* was introduced and is expanding its range on the west coast of North America. Mol. Ecol. 18: 817–833. http://dx.doi.org/10.1111/j.1365-294X.2008.04030.x

Smith ME, Douhan GW, Rizzo DM. 2007. Intra-specific and intra-sporocarp ITS variation of ectomycorrhizal fungi as assessed by rDNA sequencing of sporocarps and pooled ectomycorrhizal roots from a *Quercus* woodland. Mycorrhiza 18: 15–22. http://dx.doi.org/10.1007/s00572-007-0148-z

Tamura K, Dudley J, Nei M, Kumar S. 2007. MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) software version 4.0. Mol. Biol. Evol. 24: 1596–1599. http://dx.doi.org/10.1093/molbev/msm092

Trotter A. 1925. Supplementum universale, pars X. *Basidiomycetae.* Sylloge Fungorum 23. 1026 p.

Tulloss RE. 2011. "Studies in the *Amanitaceae*". http://www.amanitaceae.org/?Amanita calyptratoides. Retrieved 05/25/2011

Wood M, Stevens F. 2009. "California Fungi: *Amanita lanei*". MykoWeb. http://www.mykoweb.com/CAF/species/Amanita_lanei.html. Retrieved 05/25/2011

Zeller SM. 1931. *Amanita calyptrata* and *Amanita calyptroderma*. Mycologia 23: 225–226. http://dx.doi.org/10.2307/3753963